

Europe's top 10 invasive species: relative importance of climatic, habitat and socio-economic factors

BELINDA GALLARDO¹

Aquatic Ecology Group, Department of Zoology, University of Cambridge

Downing Street, Cambridge, CB2 3EJ, UK

¹ Current address: Belinda Gallardo, Integrative Ecology Department, Doñana Biological Station (EBD-CSIC), Avda. Américo Vespucio s/n, 41092 Seville, Spain (E-mails: belinda@ebd.csic.es; galla82@hotmail.com).

Running title: Factors affecting Europe's top 10 invasive species

14 Using a representative set of 10 of the worst invasive species in Europe, this study investigates the relative importance of climatic,
15 habitat and socio-economic factors in driving the occurrence of invasive species. According to the regression models performed, these factors
16 can be interpreted as multi-scale filters that determine the occurrence of invasive species, with human degradation potentially affecting the
17 performance of environmental filters. Amongst climate factors, minimum temperature of the coldest month was one of the most important
18 drivers of the occurrence of Europe's worst freshwater and terrestrial invaders like the red swamp crayfish (*Procambarus clarkii*), Bermuda
19 buttercup (*Oxalis pes-caprae*) and Sika deer (*Cervus nippon*). Water chemistry (alkalinity, pH, nitrate) determines the availability of habitat and
20 resources for species at regional to local levels and was relevant to explain the occurrence of aquatic and semi-aquatic invaders such as the
21 brook trout (*Salvalinus fontinalis*) and Canada goose (*Branta canadensis*). Likewise, nitrate and chlorophyll-*a* concentration were important
22 determinants of marine invaders like the bay barnacle (*Balanus improvisus*) and green sea fingers (*Codium fragile*). Most relevant socio-
23 economic predictors included the density of roads, country GDP, distance to ports and human influence on ecosystems. These variables were
24 particularly relevant to explain the occurrence of the zebra mussel (*Dreissena polymorpha*) and coypu (*Myocastor coypu*), species usually
25 associated to disturbed environments. The Japanese kelp (*Undaria pinnatifida*) was generally distributed much closer to ports than the other
26 two marine organisms, although insufficient information on human impacts prevented a correct assessment of the three marine species. In
27 conclusion, this study shows how socio-economic development is associated with the presence of the top 10 worst European invasive species

28 at a continental scale; and relates this fact to the provision and transport of propagules and the degradation of natural habitats that favour the
29 establishment of invasive species.

30 KEY WORDS: cold tolerance, country GDP, Europe, human influence index, logistic model, port, road density.

31

INTRODUCTION

The pan-European project DAISIE (www.europe-aliens.org) reported that a total of 12 000 non-native species are currently present in Europe, which is probably an underestimation of the real figure (DAISIE 2009). Some of the most abundant groups include plants, fish and crustaceans that come predominantly from Asia and the Americas. Their mechanisms of introduction are variable depending on the species but they are all directly or indirectly related to global trade, transport and human presence. Moreover, in their invaded range species tend to be associated with human-modified ecosystems – such as urban or agricultural lands - stressing the link between invasive species and socio-economic development (DAISIE 2009). Amongst the thousands of invasive species currently thriving in Europe, VILÀ et al. (2010) identified the top 10 worst organisms in terms of variety of ecological and economic impacts. The list included four terrestrial: the Canada goose (*Branta canadensis* Linnaeus 1758), Sika deer (*Cervus nippon* Temminck 1838), coypu (*Myocastor coypus* Molina 1782) and Bermuda buttercup (*Oxalis pes-caprae* Linnaeus 1753); three freshwater: the zebra mussel (*Dreissena polymorpha* Pallas 1771), red swamp crayfish (*Procambarus clarkii* Girard 1852) and brook trout (*Salvelinus fontinalis* Mitchill 1814); and three marine organisms: the bay barnacle (*Balanus improvisus*, Darwin 1854), green sea fingers (*Codium fragile tomentosoides* P.C. Silva 1955) and Japanese kelp (*Undaria pinnatifida* (Harvey) Suringar 1873). These top 10 species have numerous multilevel impacts. As way of example, *P. clarkii* has decimated its European counterparts through competition and parasite transmission (HOLDICH & PÖCKL 2007); the costs associated to remove *D. polymorpha* from intake pipes and other water facilities

46 are multimillion (ORESKA & ALDRIDGE 2011); both *C. nippon* and *B. canadensis* are known to hybridize with native species, posing a serious threat
47 to the conservation of genetic diversity (CORBET & HARRIS 1991; REHFISCH et al. 2010). A complete discussion on the impacts on ecosystem
48 services of these 10 representative species can be found in McLAUGHLAN et al. (2013). In spite of multiple calls from the research community to
49 increase our understanding of biological invasions (most recently, SIMBERLOFF 2013), almost nothing is known about the large scale factors
50 driving the distribution of 90% of Europe's worst invasive species (VILÀ et al. 2010). This study makes use of this representative list of 10 species
51 to investigate the relative importance of climatic, habitat and socio-economic factors in driving the large scale occurrence of invasive species in
52 Europe.

53 Temperature and precipitation are major climatic constraints to the global distribution of species that have traditionally been used to
54 delineate the biogeographic regions available to certain species (HIJMANS & GRAHAM 2006). However, invasive species have often challenged the
55 idea of a fixed environmental niche by expanding their areas of distribution towards new climates, exhibiting extraordinary adaptation
56 capabilities (PEARMAN et al. 2008). Climate may thus be insufficient to accurately describe the potential distribution of invasive species. Habitat
57 characteristics such as geomorphology, water chemistry and vegetation condition are also important regional scale determinants of invasive
58 species occurrence (Loo et al. 2009). However, drivers controlling the global-scale spread of invasive species fundamentally differ from native
59 species in that their transport and introduction depend on socio-economic activities (PYŠEK et al. 2010; ESSL et al. 2011). Transport, trade and

60 tourism are directly associated with the pathways of introduction and eventually the establishment and spread of invasive species (HULME
61 2009). For instance sea ports, a classic symbol of trade and economic development, are important gateways for invasive species that arrive as
62 imports (e.g. plants and animals), contaminants of products (e.g. timber pathogens) or stowaways (e.g. ship hull fouling or transport with
63 ballast water) (HULME 2009). Roads, railways and canals represent potential corridors along which invasive species spread with and without
64 human intervention (HULME et al. 2009). As well as providing an entrance point, ports, roads, railways and canals are highly disturbed areas,
65 providing an artificial environment where invasive species can establish and increase in abundance (BAX et al. 2003). Consequently, socio-
66 economic factors can be related not only to transport and propagule pressure, but also to the vulnerability of ecosystems to invasion, since
67 invasive species are tolerant to a wider range of environmental stress and are often able to capitalize the excess of nutrients derived from
68 human activities. For instance, population density and human wealth have been associated with increasing rates of invasion both at
69 continental (e.g. TAYLOR & IRWIN 2004; PYŠEK et al. 2010) and national (e.g. KELLER et al. 2009) scales, as they are associated with a more intense
70 use of ecosystems and habitat degradation. Furthermore, recent investigations suggest that current spatio-temporal patterns of invasion are
71 the result of economic activity and the following species invasions from decades ago (sensu invasion debt, ESSL et al. 2011). We should
72 therefore expect that the probability of invasion be due jointly to factors related to climate, habitat and socio-economic development, all of
73 which need to be integrated in risk assessments (PYŠEK et al. 2010; GALLARDO & ALDRIDGE 2013).

74 While the relationship between invasive species and socio-economic factors has been explored before, studies have been mostly
75 conducted at the local scale; and when using large continental scales, they have often relied on regional or country-level information (e.g.
76 TAYLOR & IRWIN 2004; PYŠEK et al. 2010). By using geographical information at a high resolution (1 km²), this study provides accurate insights into
77 the geographic correlation between invasive species occurrence and several climate, habitat and socio-economic indicators at a continental
78 scale.

79 METHODS

80 *Data gathering*

81 *Species occurrence*

82 Geo-referenced information on the top 10 worst invasive species occurrence in Europe (latitude and longitude coordinates) was
83 obtained from internet data gates such as the Global Biodiversity Information Facility (GBIF, <http://data.gbif.org>), the Biological Collection
84 Access Service for Europe (BioCase, <http://www.bioCase.org>), Discover Life (<http://www.discoverlife.org/>), the Ocean Biogeographic
85 Information System (OBIS, <http://www.iobis.org/>), the Census of Marine Life (COML, <http://www.coml.org/>), and the Botanical Society of the
86 British Isles (BSBI, <http://www.bsbi.org.uk/>). The reliability of resulting occurrence maps was checked against distribution maps published by

87 DAISIE (www.europe-alines.org). As a result, a total of 19 075, 2390 and 5007 data points were extracted for freshwater, terrestrial and marine
88 species respectively.

89

90 *Explanatory predictors*

91 Variables considered as potential relevant indicators of species occurrence were divided into three sets: climate, habitat and socio-
92 economic. All continental maps were downloaded at the highest spatial resolution available: 30 arcseconds, which corresponds approximately
93 to 1 km². For the marine environment, only habitat and socio-economic variables could be retrieved at 5 arcminute (ca 100 km²) resolution.

94

95 *Climatic factors.* A set of eight climatic variables were obtained from Global Climate Data (WorldClim, <http://www.worldclim.com>):
96 maximum temperature of the warmest month (Max T), minimum temperature of the coldest month (Min T) and temperature seasonality (T
97 season), annual rainfall (Annual PP), and rainfall of the driest (Min PP) and wettest (Max PP) months. Selected climate variables showed
98 relatively low levels of inter-correlation (Pearson product coefficient $r < 0.7$) overall considering the close relationship that can be expected
99 amongst them. Climatic factors are known to constrain species distribution at a global scale (MOKANY & FERRIER 2010), are pertinent to both
100 terrestrial and aquatic taxa, and are thus reliable indicators to investigate invasive species occurrence at large continental scales.

101

102 *Habitat factors.* A layer containing altitude was also obtained from WorldClim. In addition, a number of habitat-related variables were
103 used, including latitude and longitude, NDVI (NASA Goddard Earth Sciences and Information Services Center, <http://disc.gsfc.nasa.gov/>), and
104 water chemistry (e.g. pH, alkalinity, and nitrate concentration, Geochemical Atlas of Europe, www.gtk.fi). Several studies have found the
105 abundance and diversity of invasive species to follow clear altitudinal and latitudinal gradients (e.g. ALCARAZ et al. 2005; LIU et al. 2005; PINO et
106 al. 2005) because these geographic variables act as proxies of local environmental conditions — such as temperature and vegetation — that
107 affect species survival (AUSTIN 1980). Geographic variables were also included in analyses to account for the spatial variability and clustering of
108 occurrence data due to regional gradients (PINO et al. 2005). Water chemistry is expected to be relevant to explain the occurrence of
109 freshwater species in the top 10 (such as *S. fontinalis*, *D. polymorpha* and *P. clarkii*).

110 For the marine environment, a set of variables was extracted from NASA Ocean Color Web (<http://oceancolor.gsfc.nasa.gov/>), the
111 Simple Ocean Data Assimilation (SODA, <http://www.atmos.umd.edu/~ocean/>) and the National Oceanographic Data Center
112 (<http://www.nodc.noaa.gov>) including: bathymetry (Bathym.), slope, Photosynthetically Available Radiation (PAR), particulate organic carbon
113 (POC), chlorophyll *a*, turbidity, salinity, dissolved oxygen concentration (DO) and mean sea surface temperature (Temperature). Further details
114 can be found in TYBERGHEIN et al. (2012). These variables set the fundamental habitat conditions for marine species and are expected to be
115 closely linked to the distribution of the three marine invaders included in the top 10 list. Latitude and longitude were also included as variables
116 reflecting the geographic distribution of marine species.

117

118 *Socio-economic factors.* Several socioeconomic layers were used to reflect the economic richness of countries, human impacts on
119 natural ecosystems and propagule pressure. First, the Human Influence Index (HII) was obtained from the Socio Economic Data and Application
120 Centre (SEDAC, <http://sedac.ciesin.org>). This layer is a combination of factors presumed to exert an influence on ecosystems: urban extent,
121 population density, land cover, night lights and distance to roads, railways, navigable rivers and coastlines. Each one of these factors is assigned
122 a degradation score that is later summed up to constitute the human influence layer (SANDERSON et al. 2002), which ranges from 0 = close to
123 pristine locations, to 64 = much degraded areas. This map is expected to be relevant to explain the large scale distribution of the top 10
124 invaders because human activities responsible for the introduction of invasive species are more frequent in densely populated areas, land-use
125 pressure can decrease the capacity of natural environments to buffer human activities (including biological invasions) and transport routes
126 provide pathways along which species can disperse (GALLARDO & ALDRIDGE 2013). Although partially accounted for within HII, the density of
127 human population (Population, Oak Ridge National Laboratory, ORNL, <http://www.ornl.gov/>) was included as a separated layer because it has
128 been successfully used before to assess the large scale distribution of invasive species (e.g. PYŠEK et al. 2010). In addition, Gross Domestic
129 Product (GDP) was obtained for each European country from the International Monetary Fund (IMF, <http://www.imf.org>). Three distance
130 layers were generated: closeness to the coastline, ports and reservoirs. To that end, a map delineating the European coastline was obtained
131 from the official ESRI repository (<http://www.esri.com/>); a list of the most important commercial ports of the world (volume traded > 10

132 megatonnes) was extracted from the American Association of Port Authorities (AAPA, <http://www.aapa-ports.org/>); and a list of dams with a
133 capacity > 1km³ was extracted from the Global Water Systems Project (GWSP, <http://www.gwsp.org/>). Coastal landscapes, particularly in the
134 vicinity of ports, are being transformed as a consequence of the increasing demand for infrastructures to sustain residential, commercial and
135 tourist activities. Thus, intertidal and shallow marine habitats are largely being replaced by a variety of artificial substrata (e.g. breakwaters,
136 seawalls, jetties) that are very susceptible to invasion (AIROLDI & BULLERI 2011). Likewise, reservoir construction is known to facilitate the
137 introduction and establishment of freshwater invaders by providing easy public access to disturbed habitats (HAVEL et al. 2005; KELLER et al.
138 2009). The linear distance from any given pixel to the closest coastline, port or reservoir was calculated using the Spatial Analyst toolbox of
139 ArcGIS 10.0 (©ESRI). Finally, the density of roads and railways were calculated using the Spatial Analyst toolbox from linear maps obtained at
140 the ArcGIS Resource Center (<http://resources.arcgis.com>).

141 For the marine environment, only two human-related factors could be incorporated to this study: the human impact to marine
142 ecosystems and distance to commercial ports. The Global Map of Human Impacts to Marine Ecosystems (HIM, National Centre for Ecological
143 Analysis and Synthesis, NCEAS, <http://www.nceas.ucsb.edu/globalmarine/>) is similar to the HII used for freshwater and terrestrial species. This
144 map summarises information on 17 human activities that directly or indirectly have an impact on marine ecosystems such as fishing, shipping,
145 pollution, location of benthic structures and population pressure. Additionally, the linear distance to the closest port in the marine
146 environment was calculated as described above for the continental environment. Port waters might be more prone for invasion because they

147 are usually warm, nutrient rich, with available substrates to settle and potentially high propagule pressure (GALLARDO et al. 2013a). In addition
148 to HIM and port proximity, chlorophyll-*a* is commonly used as indicator of eutrophication resulting from coastal activities (i.e. agriculture,
149 aquaculture, sewage) (FERREIRA et al. 2011), and was therefore used as indirect proxy for the socio-economic influence on marine habitats.

150

151 Information on the conditions currently tolerated by Europe's top 10 invasive species at each of their known locations was extracted
152 from the above described maps using the Spatial Analyst toolbox at ArcGIS 10.0. As a result, a data matrix of species occurrence and
153 explanatory variables was obtained that was later analysed through uni- and multi-variate statistical techniques. It should be noted that the
154 data extracted from invasive species occurrence points in Europe represent the conditions of the invaded range in this continent, and not the
155 native range or invaded range of the species elsewhere (with the exception of the zebra mussel, *D. polymorpha*, whose native range comprises
156 several eastern European countries included in the calculations).

157 *Statistical analyses*

158 *Major drivers of Europe's top 10 invasive species collectively*

159 A principal component analysis (PCA) was used to identify the main environmental and socioeconomic gradients driving the occurrence
160 of the 10 species investigated collectively. PCA-axes' scores were further used to analyse differences in the environmental range of the 10

161 species. Two PCAs were developed: one for the continental (freshwater and terrestrial species) and another for the marine environment.

162 Because of the high number of data points used for calibrating PCAs (19 074 and 5807 for terrestrial and marine species respectively), boxplots

163 were used to illustrate the position of each of the 10 species along PCA's first axis of variation.

164

165 *Major drivers of Europe's top 10 invasive species individually*

166 Logistic Regression Models were used to identify the main factors explaining the presence in Europe of each of the 10 invasive species

167 evaluated. Dealing with presence-only data constituted one of the main challenges of this study. Presence-only data is being increasingly used

168 in the literature to investigate the habitat preference of invasive species, because there is often little or no information on species absence

169 available from systematic surveys (ELITH & LEATHWICK 2007). A common approach is to first create "pseudo-absences", usually achieved by

170 randomly choosing point locations in the region of interest and treating them as absences. Then the presence/pseudo-absence dataset is

171 analysed using standard analysis methods for presence/absence data (PEARCE & BOYCE 2006; ELITH & LEATHWICK 2007). In this study, 5000 random

172 pseudo-absences were generated across Europe (i.e. the European continent excluding Russia and Turkey). This figure was chosen because the

173 species investigated showed on average 4800 occurrence points per species. Pseudo-absences represent the variation in climate, habitat and

174 socio-economic covariates available to the species across Europe.

175 First, individual logistic models were fitted using the presence-absence of species as response variable, and each of the climatic habitat
176 and socio-economic variables as predictors. Plots were used to further investigate the shape of the relationship.

177 Afterwards, multiple regression models were calculated using all climatic, habitat and socio-economic factors together as explanatory
178 variables. Variables were sequentially removed and the model with the lowest Akaike Information Criterion (AIC) was selected until reaching a
179 “minimum adequate model” (CRAWLEY 2005). Although this stepwise procedure of variable selection does not test for every possible
180 combination of explanatory variables, it helps to remove variables that are not relevant to explain the species occurrence, or that are
181 redundant. Because explanatory variables were expressed in different units, standard coefficients (i.e. scaled to 0-1 so coefficients are not
182 affected by differences in units) were used to allow comparison of the relative importance of each of the variables in the model. The frequency
183 that each factor was included in uni- and multi-variate regression models was finally used as an indicator of its importance to explain the large
184 scale distribution of Europe’s top 10 invasive species. All statistical analyses were performed with MiniTab® 16 (Minitab Inc., State College PA).

RESULTS

General characteristics of invasive species locations

Data on the climate, habitat and socio-economic conditions of locations inhabited by Europe's top 10 invaders is summarized in Table 1. Amongst species, *O. pes-caprae* illustrated preference for warm and dry climates at the south-westernmost locations; whereas *M. coypu* showed the lowest temperature and highest precipitation values across species. *Dreissena polymorpha* showed a strong association with high levels of human influence, proximity to commercial ports, intensely populated areas and high road/railway density. In contrast, the brook trout *S. fontinalis* was associated with low human influence scores, population and road density. Marine species showed very variable human influence scores, with average values in general much lower than those of terrestrial species. Amongst them, *U. pinnatifida* was generally distributed much closer to ports than the other two marine organisms.

Major drivers of Europe's top 10 invasive species jointly

The continental-PCA relating all variables with the occurrence of the seven targeted freshwater and terrestrial species was significant and explained a total of 43.5% of the initial variance in its first and second axes. First axis was positively related with minimum annual temperature and several socio-economic indicators such as the density of roads and the country GDP together with water chemistry variables

198 indirectly related to high levels of human disturbance such as alkalinity and nitrate (Fig. 1A). We interpret this gradient as reflecting propagule
199 pressure, with increasing economic development at positive coordinates discriminating species frequently found in urban and suburban
200 environments such as *D. polymorpha*, *M. coypu* and *C. nippon* (Fig. 2A).

201

202 Similarly, the two first axis of the marine-PCA explained 42.6% of the initial variability in the occurrence of marine invaders. First axis
203 was positively related to water salinity and negatively to dissolved oxygen and PAR (Fig. 1B). Chlorophyll-*a*, an indirect indicator of
204 eutrophication, was positively related to the second axis. These two axes separated *C. fragile* and *U. pinnatifida* at higher coordinates from *B.*
205 *improvisus* (Fig. 2B). The other human-related variables included in this PCA — human influence and closeness to port — showed very low
206 scores in the first and second PCA axes.

207 *Major drivers of each Europe's top 10 invasive species independently*

208 Univariate logistic models identified minimum and maximum annual temperature, latitude and longitude, alkalinity and human
209 influence as the variables most significantly related to the occurrence of the seven freshwater and terrestrial species investigated. Fig. 3
210 illustrates the response of *D. polymorpha*'s probability of presence to varying levels of these factors, used as a representative example. Graphs
211 corresponding to the other nine species can be consulted in Appendices 1-9 (available online). Invasive species consistently showed an

212 increased probability of occurrence with increasing minimum temperature (Fig. 3B, with the exception of *B. canadensis*) and decreasing
213 maximum temperature (Fig. 3C, except *O. pes-caprae* typical of warm southern climates as shown in Table 1). Alkalinity favoured aquatic
214 species such as *D. polymorpha* (Fig. 3E) and *M. coypu*, but not *S. fontinalis* or *P. clarkii* (Appendix 5). All species showed a consistent positive
215 logistic response to increasing levels of human influence (Fig. 3F and Appendix 1-5). Regarding marine species, both *B. improvisus* and *C. fragile*
216 showed a significant positive response to the concentration of chlorophyll-*a* and particulate organic carbon (Appendix 6). The probability of *C.*
217 *fragile* occurrence was also highest in shallow areas close to commercial ports (Appendix 6). No significant univariate logistic model was found
218 for *U. pinnatifida*, even though occurrence locations were predominantly located in shallow areas close to ports, at low levels of human
219 influence, and high concentration of chlorophyll-*a* and organic carbon (Table 1).

220

221 Multivariate regression models showed that, for freshwater and terrestrial species, the amount of variability that can be explained by all
222 the factors included in this study ranged from 21% for *S. fontinalis* to 98% for *O. pes-caprae* (Table 2). In agreement with the univariate models
223 described before, minimum temperature and geographic location (altitude, latitude and longitude) were important factors explaining the
224 occurrence of Europe's top freshwater and terrestrial invaders. Amongst socio-economic indicators, port closeness and GDP were also relevant
225 predictors. Surprisingly, the human influence index and human population were only considered significant in four and three models
226 respectively (Table 2).

227 Marine multivariate regression models explained a lower fraction (11 to 50%) of the species occurrence variability. Latitude and
228 turbidity were negatively related to the probability of occurrence of *U. pinnatifida* and *B. improvisus*, whereas *C. fragile* was positively related
229 to shallowness, and the concentration of chlorophyll-*a* and particulate organic carbon. Surprisingly, port closeness was not included in any
230 multivariate marine model, despite species being generally located in the vicinity of ports. Human influence contributed significantly to *U.*
231 *pinnatifida* and *C. fragile* models.

232

233 The frequency that each variable was included in uni- and multi-variate regression models was used as an indicator of its importance
234 (Figs 4-5). Climatic variables, mostly minimum and maximum annual temperatures, were most important to discriminate invaded from un-
235 invaded continental regions and were therefore included in a similar number of uni- and multi-variate models (Fig. 4). Something similar could
236 be observed with latitude, longitude and alkalinity. However, socio-economic variables were more frequently included in multivariate than
237 univariate models. For instance, closeness to reservoirs and population density were not significantly related to any of the seven freshwater
238 and terrestrial species individually, and yet these variables were significantly kept in five and three multivariate models respectively. Likewise,
239 the relevance of human influence was better appreciated when used in combination with other variables in multivariate marine models, not
240 being able to significantly explain species occurrence by itself. Primary productivity was clearly the most important determinant of marine
241 bioinvasions according to both uni- and multi-variate models (Fig. 5).

DISCUSSION

The influence of climate and habitat factors

This study investigated the relative contribution of climatic, habitat and socio-economic factors to explain the occurrence of Europe's worst invaders. Moreover, this was done for a range of organisms from different habitats including terrestrial, freshwater and marine species. Amongst climate factors, minimum temperature of the coldest month was one of the most important drivers of the occurrence of Europe's worst freshwater and terrestrial invaders. Minimum temperature showed a high loading on PCA's first axis (Fig. 1A), and it was included in six out of seven univariate and all seven multivariate regression models (Fig. 4). In particular, minimum temperature above 0 °C increased over 50% the probability of occurrence of invaders (Fig. 3B). The role of cold temperature in shaping the distribution of species has been recently highlighted by ARAUJO et al. (2013), who after reviewing a large set of endotherms, ectotherms and plants concluded that the upper tolerance of species to temperature is relatively similar, with differences in the global distribution of species largely driven by their cold tolerance level. Temperature certainly affects the body size, reproduction, growth, ecological role and survival of species (GILLOOLY et al. 2001), and is a key factor in determining success in the colonization and establishment stages of invasion (THEOHARIDES & DUKES 2007). Differences in thermal tolerance of marine organisms have been also investigated by ZEREBECKI & SORTE (2011), who observed that marine invaders tended to inhabit

255 broader habitat temperature ranges and higher maximum temperatures than natives. Nevertheless, seawater temperature was only included
256 in multivariate regression models for *C. fragile* and *U. pinnatifida*.

257 Amongst habitat indicators, models for freshwater and terrestrial species highlighted the importance of geographic factors such as
258 latitude, longitude and also altitude, which achieved high loadings on PCA first axis (Fig. 1) and were included in all seven multivariate
259 regression models (Fig. 4). Geographic factors are indirect determinants of local environmental conditions — such as temperature and
260 vegetation — that affect species survival (AUSTIN 1980), and are thus commonly found to influence species distribution. For instance, ALCARAZ et
261 al. (2005) found a significant effect of latitude on the distribution of several species of fish in the Iberian peninsula; plant invasions also showed
262 clear geographic gradients in China (LIU et al. 2005) as well as in Catalonia (PINO et al. 2005). Geographic factors partially account for the spatial
263 variability of occurrence data, thus suggesting an important clustering of the 10 investigated species in Europe that is probably driven by
264 environmental preferences, dispersal limitations, or a combination of both. Regarding marine invaders, bathymetry was a prominent driver of
265 the distribution of marine invaders, which showed preference for shallow coastal areas (< 30 m deep, Table 1).

266 Apart from geographic location, water chemistry factors such as pH, alkalinity and the concentration of nitrate were also important
267 predictors for both aquatic invaders (*D. polymorpha*, *P. clarkii* and *S. fontinalis*) and semi-aquatic vertebrates (*B. canadensis* and *M. coypu*) that
268 are commonly found in salt/brackish marshes. Water chemistry determines the availability of habitat and resources for species at regional to
269 local levels and it was therefore expected to significantly contribute to the occurrence of invasive species. Results from univariate regression

models performed with data from the European wide distribution of species largely confirmed the relationship of invasive species to water chemistry reported by other authors at the local scale. For instance, an alkalinity threshold of $17 \text{ mg CaCO}_3 \text{ l}^{-1}$ has been identified to affect the reproduction and growth of *D. polymorpha* (McMAHON 1996); while *S. fontinalis* actively avoided low pH sites ($\text{pH} < 4.5$) for spawning (JOHNSON & WEBSTER 1977); pollution caused by high alkalinity and nitrate concentration has been related to the occurrence of successful aquatic invaders, which benefit from the increased ionic concentration and impoverished native communities (ARBACIAUSKAS et al. 2008). Likewise, nitrate and chlorophyll-*a* concentration were important determinants of marine bioinvasions, which might be explained by their direct relationship to the availability of food resources, and indirectly to their correlation with pollution in highly populated coastal areas.

The influence of socio-economic factors

According to the statistical models performed, the density of roads, country GDP, distance to ports and human influence were some of the most relevant predictors of invasion. The density of roads can be interpreted both as a vector of species spread and an indicator of economic development. In other words, the higher the road density in a particular region, the higher the propagule pressure directly (road transport, frequency of visits) and indirectly (human degradation, presence of other infrastructure and economic development). Many authors have described the role of roads as facilitators of invasions for plants (FLORY & CLAY 2009; MORTENSEN et al. 2009; BARBOSA et al. 2010; JOLY et al. 2011), but rarely for other types of organisms (CAMERON & BAYNE 2009). Road density showed a particularly high R^2 in *D. polymorpha*'s

284 univariate model (not shown), and a high standard coefficient in the multivariate model (Table 2). The overland spread of this species is mostly
285 related to the movement of boats and fishing gear between lakes (CARLTON 1993; ALDRIDGE et al. 2004; BOSSENBROEK et al. 2007), which may
286 explain the particular importance of road connectivity in this species model.

287 Country GDP and population density have been identified before as main predictors of invasive species richness both at national (e.g. in
288 the UK, KELLER et al. 2009) and continental (e.g. Europe, PYŠEK et al. 2010) scales. Our study further confirms the critical effect of economic
289 wealth and population density on species invasions regardless of the taxonomic group and habitat invaded. GDP was included in six out of
290 seven multivariate models and was an important contributor to *D. polymorpha* and *M. coypus* univariate models. In contrast, population
291 density had a lower impact than expected: it was only included in the *B. canadensis*, *D. polymorpha* and *P. clarkii* multivariate models, and even
292 then showing low standard coefficients. This might reflect low population density in the locations where species are present, which are
293 nonetheless in the proximity of highly populated areas. It would make more sense therefore to use an alternative indicator reflecting the
294 population density in a particular distance to an occurrence point or the distance to the closest urban area, rather than the real point value.

295 Finally, the human influence index proved to be a very promising indicator combining several degradation-related factors such as urban
296 development, night lights, population density, and distance to roads, railways and navigable rivers. In a recent risk assessment, invasive species
297 showed a consistent positive logistic response to human influence, suggesting that they display especially high invasion success in disturbed
298 environments that are characterized by simplified communities, little competition or predation and abundant organic matter (GALLARDO &

299 ALDRIDGE 2013). However because it is a combined layer, it is difficult to disentangle how the different factors accounted for by the human
300 influence index affect invasive species separately.

301 The effect of human-related factors on marine species was more difficult to address because only two indicators could be incorporated
302 — distance to ports and human degradation — neither of which proved to be of much relevance. While marine invasive species are usually
303 related to ports (BAX et al. 2003; SEEBENS et al. 2013), the variable reflecting distance to ports was only included in *U. pinnatifida*'s model, and
304 even then with a relative low coefficient. The combination of multiple factors potentially affecting the presence of invaders in the marine
305 human influence layer (such as shipping, pollution and the location of benthic structures) makes it difficult to discern their specific effect, and
306 might have an overall confounding effect. Other marine factors highlighted in the literature that could account for the unexplained variance
307 include the density of shipping routes (KALUZA et al. 2010), distance between origin and recipient ports (SEEBENS et al. 2013), presence of
308 fisheries (COPP et al. 2007), anthropogenic artificial structures that change disturbance regimes (AIROLDI & BULLERI 2011), and wave exposure
309 (STEFFANI & BRANCH 2003).

310 *Study conclusions*

311 Our analyses suggest that the occurrence of Europe's worst invaders is primarily limited by basic climate (temperature tolerance) and
312 habitat (geographic location) constraints, while human activities related to transport (roads, ports) and the degree of human impact (GDP, HII)

313 seem to play a secondary though decisive role in their final distribution. Thus climate, habitat and socio-economic development can be
314 interpreted as multi-scale filters that determine the occurrence of invasive species, as already suggested by COLAUTTI et al. (2006). Under classic
315 landscape filter theory, the species present at a particular site are the result of environmental filters acting at different scales (from continental
316 to microhabitat) on the global pool of species (POFF 1997). Invasive differ from native species in two main aspects. First, invasive species have
317 usually a broad native range, phenotypic plasticity, wide abiotic tolerance, fast growth, early maturity, high fecundity, effective dispersal
318 mechanisms and are generalists in their use of habitat and resources, which altogether increase the success of invasive species passing through
319 environmental filters (e.g. THEOHARIDES & DUKES 2007; DAVIDSON et al. 2011). Second, propagule pressure associated to socio-economic activities
320 acts as a complementary filter that affects the transport, colonization, establishment and spread of invasive species at multiple scales
321 (THEOHARIDES & DUKES 2007). While temperature still dominates the distribution of invasive species, socio-economic activities are revealed in this
322 study as important complementary determinants of species invasion. Furthermore, socio-economic factors were only relevant when
323 considered jointly with other climate and habitat factors, as illustrated in Figs 4-5. For instance, in a recent study the inclusion of socio-
324 economic factors to bioclimatic models resulted in a 20% increase in the probability of invasion in general and, in particular, a six-fold increase
325 in the area predicted suitable for the quagga mussel (*D. r. bugensis*, a species closely related to *D. polymorpha*) (GALLARDO & ALDRIDGE 2013). The
326 importance of socio-economic factors is likely to be because they reflect possible routes of introduction, such as ports, roads, railways and the
327 ornamental trade. Thus climate and habitat filters are complemented with a socio-economic filter intimately related to propagule pressure, all

328 of which are fundamental to understand the large-scale distribution of invasive species. Yet socio-economic activities are often omitted in risk
329 assessments because they are difficult to quantify, resulting in serious underestimation of the area at risk (GALLARDO & ALDRIDGE 2013). This
330 study therefore advocates for the use of available global information on the country richness, population density, transport networks and
331 human disturbance of ecosystems, as means to provide more accurate assessments of invasion risk.

332 *Study limitations*

333 A number of factors may affect the accuracy of regression models, some of which are related to (i) the uneven number and spatial bias
334 of occurrence points, (ii) the use of pseudo-absences instead of real absence points to calibrate regression models, (iii) high inter-correlation of
335 explanatory variables, (iv) lack of additional relevant predictors, and (v) limited number of species investigated per major habitat.

336 The number of occurrence points used to calibrate regression models varied widely between 72 for *U. pinnatifida* to over 13 000 for *B.*
337 *canadensis*. Both the number and distribution of occurrences are important in models, since the ratio between presence and absence data and
338 spatial bias of observations affects the ability of the model to discriminate between invaded and un-invaded areas. Spatial clustering of a large
339 amount of data around particular geographic regions may actually explain the high importance of geographic factors (latitude and longitude) in
340 this study, most conspicuously in the case of *O. pes-caprae* and *B. canadensis*. Although techniques exist to reduce the spatial clustering of
341 species data, recent investigations recommend using all available spatial information on invasive species to avoid underestimating their

342 potential distribution (GALLARDO et al. 2013b). On the other hand, models should be greatly affected by the use of randomly selected pseudo-
343 absence instead of real absence data (LOBO et al. 2010). Such information is usually not available for invasive species, and even when it is, it is
344 usually not reliable as un-invaded locations can be invaded in the future, or might be already affected by the invasive species that remain so far
345 unnoticed. The generation of pseudo-absences is nevertheless commonly accepted when using other correlational approaches such as species
346 distribution models (BARBET-MASSIN et al. 2012), and is considered to provide the best available approximation to investigate major differences
347 in climate, habitat and socio-economic conditions between invaded and un-invaded sites.

348 Multicollinearity among predictors may affect the reliability of multivariate methods by artificially changing variable coefficients and
349 increasing the percentage of variance explained by the model (R^2). For this reason, variables included in this study were carefully chosen to
350 exhibit low levels of inter-correlation (Pearson $r < 0.70$, $P > 0.05$), and R^2 values adjusted for the number of predictors in the model were
351 reported. On the other hand, while backward elimination of variables helped to remove irrelevant or redundant predictors, not all possible
352 combinations of variables could be tested, which may have resulted in the over-representation of certain variables. Although the factors
353 evaluated in this study provide valuable information on the effect of socio-economic development on invasive species, the inclusion of other
354 predictors more directly related to propagule pressure and species dispersal may further improve the predictability of models. Finally, it has to
355 be noted the very limited number of invasive species investigated per major habitat, which undoubtedly limits the generality of conclusions.
356 Future studies using larger subsets of species will provide more robust insights into the preliminary patterns suggested here.

357

358 Despite these various caveats, this study provides a comprehensive overview of the relative importance of climate, habitat and socio-
359 economic factors to explain the continental scale occurrence of some of Europe's worst invaders. A range of statistical analyses were used to
360 illustrate how socio-economic development is associated with the presence of the top 10 worst European invasive species at a continental
361 scale; and this fact was related to the provision and transport of propagules and the degradation of natural habitats that favour the
362 establishment of invasive species.

363

ACKNOWLEDGEMENTS

364 The author would like to thank Drs David Aldridge and Claire McLaughlan University of Cambridge) and Dr Chris Yesson (London
365 Zoological Society) for their useful contribution to an earlier version of the manuscript. The research leading to these results has received
366 funding from the European Commission (FP7/2007-2013, Marie Curie IEF program) under grant agreement n°251785.

367

REFERENCES

- AIROLDI L. & BULLERI F. 2011. Anthropogenic disturbance can determine the magnitude of opportunistic species responses on marine urban infrastructures. *Plos One* 6: e22985.
- ALDRIDGE D.C., ELLIOTT P. & MOGGRIDGE G.D. 2004. The recent and rapid spread of the zebra mussel (*Dreissena polymorpha*) in Great Britain. *Biological Conservation* 119: 253-261.
- ALCARAZ C., VILA-GISPERS A., & GARCÍA-BERTHOU E. 2005. Profiling invasive fish species: the importance of phylogeny and human use. *Diversity and Distributions* 11: 289-298.
- ARAÚJO M.B., FERRI-YÁÑEZ F., BOZINOVIC F., MARQUET P.A., VALLADARES F. & CHOWN S.L. 2013. Heat freezes niche evolution. *Ecology Letters* 16: 1206-1219.
- ARBACIAUSKAS K., SEMENCHENKO V., GRABOWSKI M., LEUVEN R.S.E.W., PAUNOVIC M., SON M.O., CSANYI B., GUM-ULIAUSKAITE S., KONOPACKA A., NEHRING S., VAN DER VELDE G., VEZHNOVETZ V. & PANOV V.E. 2008. Assessment of biocontamination of benthic macroinvertebrate communities in European inland waterways. *Aquatic Invasions* 3: 211-230.
- AUSTIN M.P. 1980. Searching for a model for use in vegetation analysis. *Vegetatio* 42: 11-21.
- BARBET-MASSIN M., JIGUET F., ALBERT C.H. & THUILLER W. 2012. Selecting pseudo-absences for species distribution models: how, where and how many? *Methods in Ecology and Evolution* 3: 327-338.
- BARBOSA N.P.U., WILSON FERNANDES G., CARNEIRO M.A.A. & JUNIOR L.A.C. 2010. Distribution of non-native invasive species and soil properties in proximity to paved roads and unpaved roads in a quartzitic mountainous grassland of southeastern Brazil (rupestrian fields). *Biological Invasions* 12: 3745-3755.

386 BAX N., WILLIAMSON A., AGUERO M., GONZALEZ E. & GEEVES W. 2003. Marine invasive alien species: a threat to global biodiversity. *Marine*
387 *Policy* 27: 313-323.

388 BOSSENBROEK J.M., JOHNSON L.E., PETERS B. & LODGE D.M. 2007. Forecasting the expansion of zebra mussels in the United States.
389 *Conservation Biology* 21: 800-810.

390 CAMERON E.K. & BAYNE E.M. 2009. Road age and its importance in earthworm invasion of northern boreal forests. *Journal of Applied*
391 *Ecology* 46: 28-36.

392 CARLTON J. 1993. Dispersal mechanisms of the Zebra Mussel (*Dreissena polymorpha*), pp. 677-697. In: Nalepa, T.F. & Schloesser, D.W.
393 Zebra Mussels: Biology, impacts, and control. *Boca Raton, FL: Lewis Publishers*.

394 COLAUTTI R.I., GRIGOROVICH I.A. & MACISAAC H.J. 2006. Propagule pressure: a null model for biological invasions. *Biological Invasions* 8:
395 1023-1037.

396 COPP G.H., TEMPLETON M. & GOZLAN R.E. 2007. Propagule pressure and the invasion risks of non-native freshwater fishes: a case study in
397 England. *Journal of Fish Biology* 71: 148-159.

398 CORBET G. & HARRIS S. 1991. The handbook of British mammals, Third edn. *Oxford (UK): Blackwell Scientific Publications*.

399 CRAWLEY M.J. 2005. Statistics: An introduction using R. *London (UK): John Wiley & Sons Ltd*.

400 DAISIE 2009. Handbook of alien species in Europe. *Knoxville, TN (USA): Springer*.

401 DAVIDSON A.M., JENNIONS M. & NICOTRA A.B. 2011. Do invasive species show higher phenotypic plasticity than native species and, if so, is it
402 adaptive? A meta-analysis. *Ecology Letters* 14: 419-431.

403 ELITH J. & LEATHWICK J. 2007. Predicting species distributions from museum and herbarium records using multiresponse models fitted with
404 multivariate adaptive regression splines. *Diversity and Distributions* 13: 265-275.

405 ESSL F., DULLINGER S., RABITSCH W., HULME P.E., HUELBER K., JAROSIK V., KLEINBAUER I., KRAUSMANN F., KUEHN I., NENTWIG W., VILÀ M., GENOVESI P.,
 406 GHERARDI F., DESPREZ-LOUSTAU M.-L., ROQUES A. & PYŠEK P. 2011. Socioeconomic legacy yields an invasion debt. *Proceedings of the National*
 407 *Academy of Sciences of the United States of America* 108: 203-207.

408 FERREIRA J.G., ANDERSEN J.H., BORJA A., BRICKER S.B., CAMP J., CARDOSO DA SILVA M., GARCÉS E., HEISKANEN A.-S., HUMBORG C. & IGNATIADES L. 2011.
 409 Overview of eutrophication indicators to assess environmental status within the European Marine Strategy Framework Directive. *Estuarine,*
 410 *Coastal and Shelf Science* 93: 117-131.

411 FLORY S.L. & CLAY K. 2009. Effects of roads and forest successional age on experimental plant invasions. *Biological Conservation* 142:
 412 2531-2537.

413 GALLARDO B. & ALDRIDGE D.C. 2013. The 'dirty dozen': socio-economic factors amplify the invasion potential of 12 high risk aquatic invasive
 414 species in Great Britain and Ireland. *Journal of Applied Ecology* 50: 757-766.

415 GALLARDO B., ZIERITZ A. & ALDRIDGE D.C. 2013a. Targeting and prioritisation for INS in the RINSE project area. *Cambridge, UK: University of*
 416 *Cambridge*.

417 GALLARDO B., ZU ERMGASSEN P.S.E. & ALDRIDGE D. 2013b. Invasion ratcheting in the zebra mussel (*Dreissena polymorpha*) and the ability of
 418 native and invaded ranges to predict its global distribution. *Journal of Biogeography* doi:10.1111/jbi.12170.

419 GILLOOLY J.F., BROWN J.H., WEST G.B., SAVAGE V.M. & CHARNOV E.L. 2001. Effects of size and temperature on metabolic rate. *Science* 293:
 420 2248-2251.

421 HAVEL J.E., LEE C.E. & VANDER ZANDEN M.J. 2005. Do reservoirs facilitate invasions into landscapes? *Bioscience* 55: 518-525.

422 HIJMANS R.J. & GRAHAM C.H. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions.
 423 *Global Change Biology* 12: 2272-2281.

424 HOLDICH D. & PÖCKL M. 2007. Invasive crustaceans in European inland waters, pp. 29-75. In: Gherardi F., Ed. Biological invaders in inland
425 waters: Profiles, distribution, and threats. Dordrecht (The Netherlands): *Springer*.

426 HULME P.E. 2009. Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology*
427 46: 10-18.

428 HULME P.E., NENTWIG W., PYŠEK P. & VILÀ M. 2009. Biological Invasions: Benefits versus risks response. *Science* 324: 1015-1016.

429 JOHNSON D.W. & WEBSTER D.A. 1977. Avoidance of low pH in selection of spawning sites by brook trout (*Salvelinus fontinalis*). *Journal of*
430 *the Fisheries Board of Canada* 34: 2210-2215.

431 JOLY M., BERTRAND P., GBANGOU R.Y., WHITE M.-C., DUBE J. & LAVOIE C. 2011. Paving the way for invasive species: Road type and the spread of
432 common ragweed (*Ambrosia artemisiifolia*). *Environmental Management* 48: 514-522.

433 KALUZA P., KOLZSCH A., GASTNER M.T. & BLASIUS B. 2010. The complex network of global cargo ship movements. *Journal of the Royal Society*
434 *Interface* 7: 1093-1103.

435 KELLER R.P., ERMGASSEN P. & ALDRIDGE D.C. 2009. Vectors and timing of freshwater invasions in Great Britain. *Conservation Biology* 23:
436 1526-1534.

437 LIU J., LIANG S.C., LIU F.H., WANG R.Q. & DONG M. 2005. Invasive alien plant species in China: regional distribution patterns. *Diversity and*
438 *Distributions* 11: 341-347.

439 LOBO J.M., JIMENEZ-VALVERDE A. & HORTAL J. 2010. The uncertain nature of absences and their importance in species distribution modelling.
440 *Ecography* 33: 103-114.

441 LOO S.E., MAC NALLY R., O'DOWD D.J., THOMSON J.R. & LAKE P.S. 2009. Multiple scale analysis of factors influencing the distribution of an
442 invasive aquatic grass. *Biological Invasions* 11: 1903-1912.

443 MCLAUGHLAN C., GALLARDO B. & ALDRIDGE D.C. 2013. How complete is our knowledge of the ecosystem services impacts of Europe's top 10
 444 invasive species? *Acta Oecologica* dx.doi.org/10.1016/j.actao.2013.03.005.

445 McMAHON R.F. 1996. The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American*
 446 *Zoologist* 36: 339-363.

447 MOKANY K. & FERRIER S. 2010. Predicting impacts of climate change on biodiversity: a role for semi-mechanistic community-level
 448 modelling. *Diversity and Distributions* 17: 374-380.

449 MORTENSEN D.A., RAUSCHERT E.S.J., NORD A.N. & JONES B.P. 2009. Forest roads facilitate the spread of invasive plants. *Invasive Plant Science*
 450 *and Management* 2: 191-199.

451 ORESKA M. & ALDRIDGE D. 2011. Estimating the financial costs of freshwater invasive species in Great Britain: a standardized approach to
 452 invasive species costing. *Biological Invasions* 13: 305-319.

453 PEARCE J.L. & BOYCE M.S. 2006. Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology* 43: 405-412.

454 PEARMAN P.B., GUIBAN A., BROENNIMANN O. & RANDIN C.F. 2008. Niche dynamics in space and time. *Trends in Ecology & Evolution* 23: 149-
 455 158.

456 PINO J., FONT X., CARBO J., JOVE M. & PALLARES L. 2005. Large-scale correlates of alien plant invasion in Catalonia (NE of Spain). *Biological*
 457 *Conservation* 122: 339-350.

458 POFF N.L. 1997. Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the*
 459 *North American Benthological Society* 16: 391-409.

460 PYŠEK P., JAROŠÍK V., HULME P.E., KÜHN I., WILD J., ARIANOUTSOU M., BACHER S., CHIRON F., DIDŽIULIS V., ESSL F., GENOVESI P., GHERARDI F., HEJDA M.,
 461 KARK S., LAMBDON P.W., DESPREZ-LOUSTAU M.-L., NENTWIG W., PERGL J., POBOLŠAJ K., RABITSCH W., ROQUES A., ROY D.B., SHIRLEY S., SOLARZ W., VILÀ M. &

462 WINTER M. 2010. Disentangling the role of environmental and human pressures on biological invasions across Europe. *Proceedings of the*
 463 *National Academy of Sciences* 107: 12157-12162.

464 REHFISCH M., ALLAN J. & AUSTIN G. 2010. The effect on the environment of Great Britain's naturalized Greater Canada *Branta canadensis*
 465 and Egyptian Geese *Alopochen aegyptiacus*. *BOU Proceedings—The Impacts of Non-native Species*. ([www.bou.org.uk/bouproc-net/non-](http://www.bou.org.uk/bouproc-net/non-natives/rehfisch-et-al.pdf)
 466 [natives/rehfisch-et-al.pdf](http://www.bou.org.uk/bouproc-net/non-natives/rehfisch-et-al.pdf))

467 SANDERSON E.W., JAITEH M., LEVY M.A., REDFORD K.H., WANNEBO A.V. & WOOLMER G. 2002. The human footprint and the last of the wild.
 468 *Bioscience* 52: 891-904.

469 SEEBENS H., GASTNER M. & BLASIUS B. 2013. The risk of marine bioinvasion caused by global shipping. *Ecology Letters* 16(6): 782-790

470 SIMBERLOFF D. 2013. Biological invasions: What's worth fighting and what can be won? *Ecological Engineering*
 471 doi:10.1016/j.ecoleng.2013.08.004.

472 STEFFANI C.N. & BRANCH G.M. 2003. Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure.
 473 *Marine Ecology-Progress Series* 246: 197-209.

474 TAYLOR B.W. & IRWIN R.E. 2004. Linking economic activities to the distribution of exotic plants. *Proceedings of the National Academy of*
 475 *Sciences of the United States of America* 101: 17725-17730.

476 THEOHARIDES K.A. & DUKES J.S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four
 477 stages of invasion. *New Phytologist* 176: 256-273.

478 TYBERGHEIN L., VERBRUGGEN H., PAULY K., TROUPIN C., MINEUR F. & DE CLERCK O. 2012. Bio-ORACLE: a global environmental dataset for marine
 479 species distribution modelling. *Global Ecology and Biogeography* 21: 272-281.

480 VILÀ M., BASNOU C., PYŠEK P., JOSEFSSON M., GENOVESI P., GOLLASCH S., NENTWIG W., OLENIN S., ROQUES A., ROY D., HULME P.E. & DAISIE PARTNERS.
481 2010. How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. *Frontiers in*
482 *Ecology and the Environment* 8: 135-144.

483 ZEREBECKI R.A. & SORTE C.J. 2011. Temperature tolerance and stress proteins as mechanisms of invasive species success. *Plos One* 6:
484 e14806.

485
486

487 Cited Web References

488

489 AAPA 2009. American Association of Port Authorities. Data available at <http://www.aapa-ports.org/>. Last accessed June 2011.

490 ArcGIS Resource Center. Available through <http://resources.arcgis.com/>. Last accessed June 2013.

491 BioCase 2005. Biological Collection Access Service for Europe. Available at <http://www.bioCase.org/>. Last accessed June 2010.

492 BSBI. Botanical Society of Britain and Ireland. Available at <http://www.bsbi.org.uk/>. Last accessed June 2010.

493 COML 2010. Census of Marine Life. Site by the Office of Marine Programs, University of Rhode Island, Graduate School of Oceanography.

494 Available at <http://www.coml.org/>. Last accessed June 2010.

495 DAISIE 2009. Delivering Alien Invasive Species Inventories for Europe. Available at <http://www.europe-aliens.org/>. Last accessed June 2013.

496 DiscoverLife 2011. Available at <http://www.discoverlife.org/>. Last accessed June 2010.

497 ESRI Repository. Available at <http://www.esri.com/>. Last accessed June 2010.

498 GAE, 1998. Geochemical Atlas of Europe. Data available at <http://www.gtk.fi/>. Last accessed June 2011.

499 GBIF 2013. Global Biodiversity Information facility. Available at <http://data.gbif.org/>. Last accessed June 2010.

500 GSWP 2009. Global Water Systems Project available at <http://www.gwsp.org/>. Last accessed June 2010.

501 IMF 2010. International Monetary Fund. Data available at <http://www.imf.org/>. Last accessed June 2011.

502 NASA-Goddard Earth Sciences and Information Services Center. Data available at <http://disc.gsfc.nasa.gov/>. Last accessed June 2011.

503 NASA-OCW. NASA Ocean Color Web at <http://oceancolor.gsfc.nasa.gov/>. Last accessed June 2013.

504 NCEAS 2008. National Centre for Ecological Analysis and Synthesis. Available at <http://www.nceas.ucsb.edu/globalmarine/>. Last accessed June

505 2013.

506 NODC-NOAA. National Oceanographic Data Center at <http://www.nodc.noaa.gov>. Last accessed June 2013.
 507 OBIS 2010. Data from the Ocean Biogeographic Information System. Intergovernmental Oceanographic Commission of UNESCO. Web.
 508 <http://www.iobis.org/>. Last accessed June 2010.
 509 ORNL 2000. Oak Ridge National Laboratory. Available at <http://www.ornl.gov/>. Last accessed June 2010.
 510 SEDAC 2004. Socio-economic Data and Applications Center. Available at <http://sedac.ciesin.columbia.edu/>. Last accessed June 2012.
 511 SODA. Simple Ocean Data Assimilation at <http://www.atmos.umd.edu/~ocean/>. Last accessed June 2013.
 512 WorldClim 2005. Global Climate Database. Free climate data for ecological modelling and GIS. Available at <http://worldclim.org/>. Last accessed
 513 February 2010.

514

515

516

517 **Table 1.** Climatic, habitat and socio-economic conditions of sites inhabited by Europe's top 10 worst invasive species. Values correspond to
 518 means of all the locations where the species is present in Europe \pm standard deviation. T: temperature, PP: precipitation, POC: Particulate
 519 Organic Carbon, PAR: Photosynthetically Available Radiation, HII: Human Influence Index, HIM: Human Influence on Marine ecosystems, GDP:
 520 Gross Domestic Product (in PPP, Purchasing Power Parity, to allow comparison). Empty cells: not applicable.

521

	<i>B. canadensis</i>	<i>C. nippon</i>	<i>D. polymorpha</i>	<i>M. coypus</i>	<i>P. clarkii</i>	<i>S. fontinalis</i>	<i>O. pes-caprae</i>	<i>B. improvisus</i>	<i>C. fragile</i>	<i>U. pinnatifida</i>
I. Climatic										
Maximum T (°C)	20.8 \pm 1.1	17.9 \pm 1.9	21.6 \pm 2.3	23.1 \pm 2.7	28.2 \pm 3.5	19.9 \pm 2.4	29.8 \pm 2.9			
Minimum T (°C)	-7.4 \pm 4.4	-13.0 \pm 1.6	-0.9 \pm 2.5	-0.2 \pm 2.1	2.1 \pm 2.7	-8.8 \pm 4.4	5.7 \pm 2.4			
T Season	7.2 \pm 1.1	4.5 \pm 0.6	5.6 \pm 1.2	5.4 \pm 0.8	5.7 \pm 0.6	7.2 \pm 1.2	5.2 \pm 0.7			
Annual PP (mm)	652 \pm 135	1183 \pm 358	752 \pm 148	727 \pm 166	659 \pm 216	760 \pm 227	544 \pm 185			
Min PP (mm)	34.4 \pm 17.3	66.3 \pm 17.3	43.4 \pm 9.6	43.2 \pm 10.5	25.4 \pm 10.9	40.6 \pm 17.7	6.1 \pm 10.9			
Max PP (mm)	77.1 \pm 14.4	134.2 \pm 48.2	80.3 \pm 17.6	79.2 \pm 22.9	83.6 \pm 27.3	91.6 \pm 17.7	83.0 \pm 10.9			
II. Habitat										
Altitude (m)	95.0 \pm 97.8	266.5 \pm 184.9	47.6 \pm 134.3	144.1 \pm 235.8	319.6 \pm 310.9	456.5 \pm 492.3	235.1 \pm 274.0			
Latitude	15.3 \pm 6.2	-3.2 \pm 3.6	6.2 \pm 9.2	3.2 \pm 5.9	0.4 \pm 5.6	11.7 \pm 5.9	38.2 \pm 3.1	53.7 \pm 2.8	54.6 \pm 3.9	48.9 \pm 3.4

Longitude	59.0±3.2	55.7±2.5	51.9±3.26	48.9±3.6	42.2±3.4	57.6±6.5	-2.7±6.31	9.1±8.87	-2.2±7.1	-1.0±4.6
Water Nitrate (mg/L)	2.8±6.2	9.4±9.5	10.7±8.7	22.5±12.9	11.1±8.8	2.5±6.2	10.5±6.1			
Water pH	6.7±0.5	7.6±0.3	7.5±0.4	7.8±0.4	7.8±0.8	6.7±0.8	8.1±0.3			
Water Alkalinity (mg/L)	47.4±53.5	76.9±70.8	237.1±92.6	202.5±80.9	205.9±92.2	50.9±70.5	234.4±66.5			
NDVI	0.6±0.1	0.6±0.1	0.6±0.1	0.6±0.1	0.6±0.1	0.6±0.1	0.05±0.02			
Sea Bathymetry (m)								-9.3±13.7	-12.0±21.3	-5.8±10.5
Sea PAR (Einstein/m ² . day)								30.4±2.4	27.9±1.9	28.7±1.3
Sea POC (mol/m ³)								737±462	529±262	530±244
Sea Chlorophyll-a (mg/m ³)								16.1±10.9	5.7±5.4	5.1±4.2
Sea Dissolved Oxygen (ml/L)								7.3±0.8	6.4±0.4	6.1±0.3
Sea Water current (m/sec)								0.004±0.6	0.5±1.4	0.01±0.6
Sea Slope								4.9±12.4	10.5±13.8	7.8±10.9
Sea Turbidity (mg/L)								9.2±3.1	10.6±2.4	12.6±2.8
Sea Salinity (PSS)								18.7±12.5	33.4±3.1	34.9±1.2
Sea mean T (°C)								9.7±1.6	10.8±1.8	12.8±1.8
III. Socio-economic										
Port (km)	276.0±1.4	140.7±3.1	122.6±3.4	173.0±3.6	204.8±8.2	339.9±6.7	204.8±8.2	170.1±124.2	200.1±129.8	111.6±132.7
Human Influence (HII and HIM)	30.6±0.1	22.5±0.2	34.5±0.3	30.8±0.3	30.6±0.8	19.0±0.4	35.9±0.6	10.15±14.73	10.14±14.32	7.8±14.96
Reservoir (km)	226.2±1.2	53.5±2.1	105.9±1.9	90.1±2.1	56.2±3.2	122.4±3.8	76.9±4.3			
Population density (Num./km ²)	119.3±4.1	34.2±7.3	367.5±25.3	124.0±12.1	207.1±90.5	20.4±7.0	244.7±42.6			
GDP x 1000	387±3.3	1548±8.7	755±12.9	1619±14.3	1309±33.5	642±25.6	990±13.2			
Road density	2.4±0.1	2.5±0.1	4.5±0.1	3.5±0.04	2.9±0.1	2.1±0.1	1.9±0.1			
Railways density	0.9±0.1	1.1±0.1	1.2±0.1	0.9±0.1	1.1±0.1	0.6±0.1	0.4±0.1			

Table 2. Results of stepwise regression models performed with the species occurrence as response variable (species real occurrences and 5000 pseudo-absences random points) and three sets of climatic, habitat and human related predictors. $R^2(\text{adj})$ = percentage of variance explained by the model, adjusted for the number of predictors included.

		<i>B. canadensis</i>	<i>C. nippon</i>	<i>D. polymorpha</i>	<i>M. coypus</i>	<i>P. clarkii</i>	<i>S. fontinalis</i>	<i>O. pes-caprae</i>	<i>B. improvisus</i>	<i>C. fragile</i>	<i>U. pinnatifida</i>
	<i>Constant</i>	6.6	1.5	2.9	1.5	0.5	2.0	0.2	1.3	2.7	0.4
I. Climatic	Bio4	-1.0	-1.9		-1.9	-1.3	0.3				
	Bio5		0.2	-0.8	0.9	0.8		0.02			
	Bio6	-1.0	-1.5	1.0	-1.8	-1.07	0.5	-0.03			
	Bio12		0.5	0.9			-0.8				
	Bio13	-0.5		-1.2	-0.3	-0.1		-0.1			
	Bio14			-0.2	0.5		0.6				
II. Habitat	Altitude	-0.7	-0.5	-0.3	-0.3	-0.2	0.3	-0.1			
	Alkalinity	-1.7	-0.3	0.4				-0.02			
	NO3		0.1	-0.4	0.7	-0.2	0.3	0.02			
	pH		0.8		0.2	-0.1	-0.5	-0.01			
	Latitude	0.3	-0.6	-0.2	-0.7	-0.4	-0.2	0.02	-1.8	-0.6	-0.6
	Longitude	2.6	0.6	0.3	-0.2	-0.5	0.9	-0.1	-0.2	-0.9	
	NDVI	-0.1	-0.2	-0.5		-0.2	0.3	-0.1			
	Chlorophyll a								0.6	1.6	0.2
	POC								0.7	1.4	0.2
	PAR								-0.4	-1.3	-0.3
	DO								0.3	0.3	
	Water Temp.									0.7	0.2
	Salinity								-0.2	0.7	0.1
	TSS								-1.5	-0.9	-0.7
	Bathymetry								0.6	1.3	0.2
	Water Current								0.1	-0.3	
III. Socio-economic	Ports	-0.9	-0.4	-0.6	-0.3	0.1	-0.3	0.03			-0.05
	Coast										
	Reservoirs	0.4	-0.2	0.1			-0.1	0.02			
	Population	0.1		0.18		0.1					
	Human influence	0.5		0.3	0.2		0.1			-0.4	-0.2
	GDP	-0.3	0.3	-0.5	0.5	0.2	0.1				
	Roads	0.5	-0.6	1.2			0.2	0.02			
	Railways		0.4	-0.4	-0.3		-0.4	-0.01			
	$R^2(\text{adj})$	0.68	0.64	0.55	0.46	0.23	0.21	0.98	0.34	0.55	0.12

Fig. 1. -- Principal Component Analysis showing the importance of climatic, habitat and socio-economic variables to explain the European distribution of (A) seven continental (freshwater and terrestrial), and (B) three marine invasive species. The two first principal components are plotted with the proportion of variance explained in the bottom right corner of the plot. Explanation of variable abbreviations can be consulted in the text.

Fig. 2. -- Boxplots representing the position of (A) seven continental (freshwater and terrestrial) and (B) three marine invasive species, along the first PCA axis of variation. PCA plots of variable importance can be consulted in Fig. 1. Explanation of variable abbreviations can be consulted in the text.

Fig. 3. -- Results from univariate logistic models performed between the presence-absence of *D. polymorpha* in Europe and (A) temperature seasonality, (B) minimum temperature, (C) maximum temperature, (D) geographic latitude, (E) Water alkalinity concentration and (F) the Human Influence Index. The F-ratio and *P*-value of each model is indicated in the bottom right corner of each plot. The shaded area around the regression line represents the SE of the model.

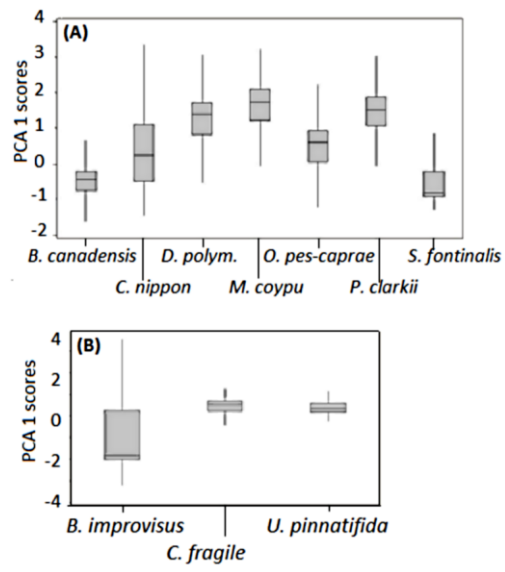
Fig. 4. -- Relative importance of climatic, habitat and socio-economic variables to explain the occurrence of seven of the worst freshwater and terrestrial invasive species in Europe. Grey bars represent the number of species showing a significant response to each variable in univariate logistic models, whereas black bars refer to multivariate logistic models. Explanation of variable abbreviations can be consulted in the text.

Fig. 5. -- Relative importance of habitat and socio-economic variables explaining the occurrence of three of the worst marine invasive species in Europe.

554 Grey bars represent the number of species showing a significant response to each
555 variable in univariate logistic models, whereas black bars refer to multivariate logistic
556 models. Explanation of variable abbreviations can be consulted in the text.

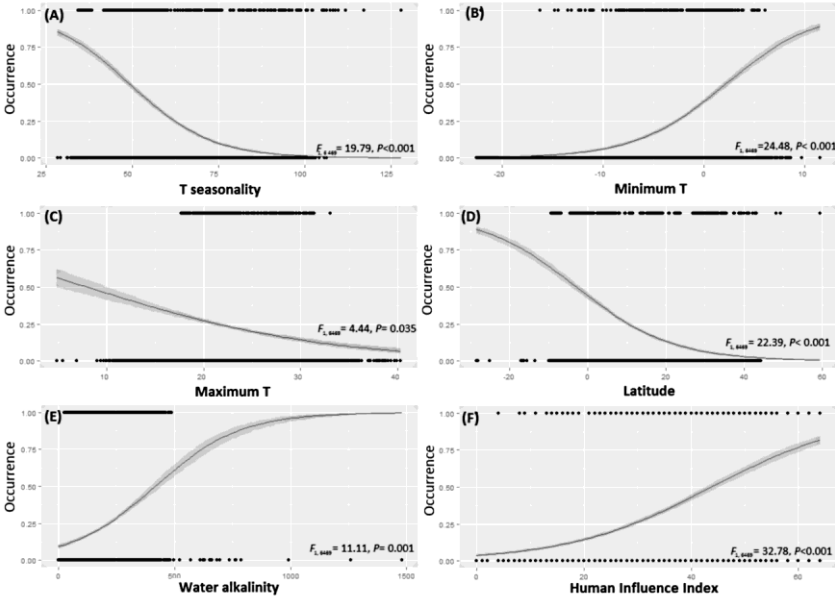
557 **Figure 1.**
558
559

Figure 2.



564

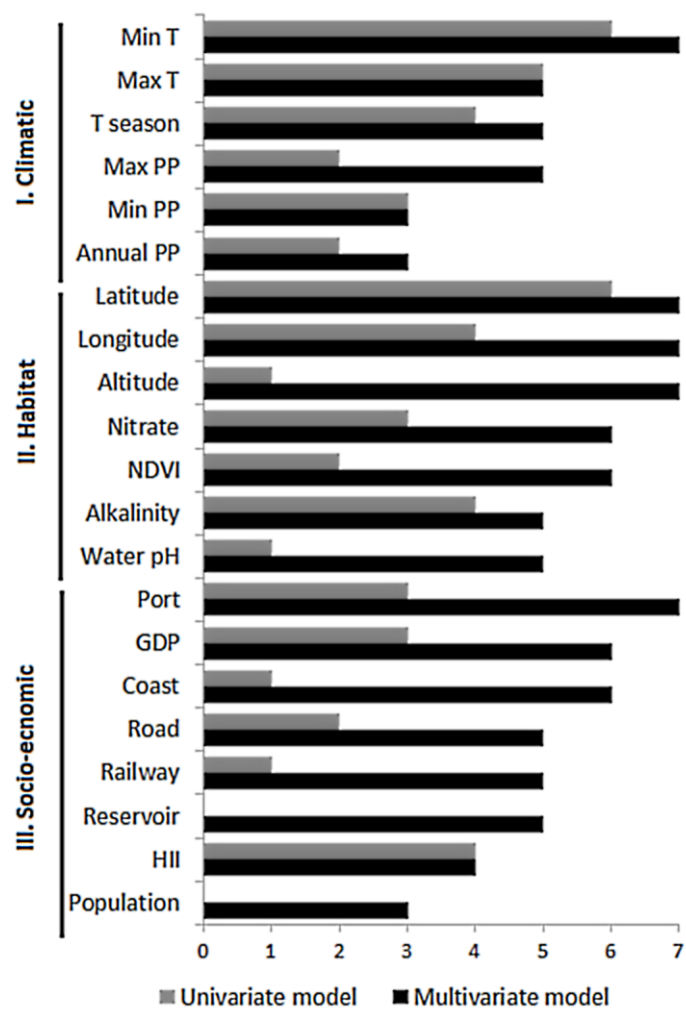
Figure 3.



565

566

Figure 4.

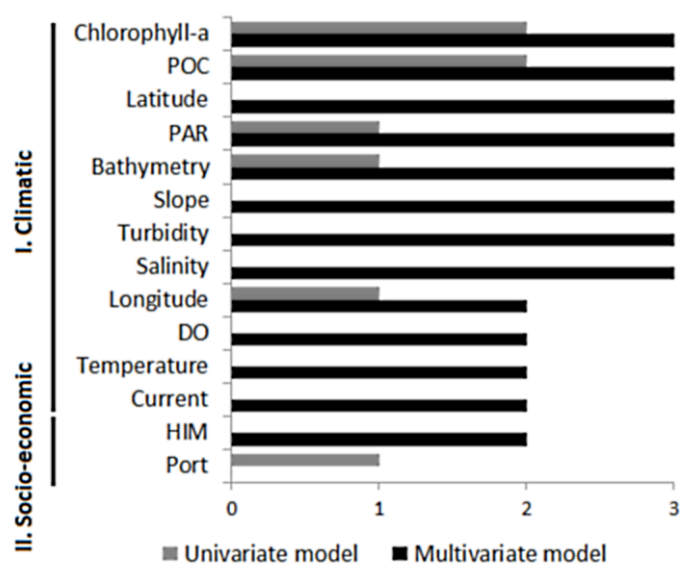


567

568

569

Figure 5.



570

571